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Three Styles in the Evolutionary Analysis of Human Behavior

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A theory does not give conclusions—it directs the nature of the research, but each application of the theory demands careful research. . . . There is no way for a scientist to leap directly from genetic or evolutionary theory to conclusions about human behavior. The principal task for the scientist is the research that links theory and conclusion.

—Sherwood L. Washburn (1978)

As the title indicates, my chapter is focused on the diversity contained within the field of inquiry surveyed in this volume. Specifically, I want to compare the approaches known as evolutionary psychology, behavioral ecology, and dual inheritance theory with respect to their key assumptions, explanatory goals, and realms of application. These distinct approaches to evolutionary analysis of human behavior have each crystallized during the twenty-plus years since Chagnon and Irons organized the 1976 American Anthropological Association symposia commemorated here—symposia which coincided roughly with the publication of E. O. Wilson's *Sociobiology* (1975) and Dawkins's *The Selfish Gene* (1976). After surveying the three approaches, I will consider why they have come to be seen as competing alternatives, and then explore to what extent it might make better sense to see them as complementary. Although most comparisons to date have been rather partisan or even polemical, and I myself am closely identified with one of the approaches (behavioral ecology), in this essay I do my best to provide an even-handed account.

EVOLUTIONARY PSYCHOLOGY

Evolutionary psychology (EP), as the name suggests, applies evolutionary reasoning to psychological phenomena. The goal of EP, as succinctly put by Symons (1992:137), is to uncover “the psychological mechanisms that underpin human . . . behavior, and . . . the selective forces that shaped those mechanisms.”

Reviews of this approach can be found in Barkow, et al. (1992), Buss (1995), and Daly and Wilson (1997).

EP embraces several key assumptions, which I will term modularity, historicity, adaptive specificity, and environmental novelty. *Modularity* posits that human behavior is guided by specialized cognitive mechanisms performing specialized tasks rather than “general purpose” mechanisms that work across multiple behavioral domains. This assumption is taken directly from contemporary cognitive psychology, and indeed most of the evidence for it is developed in that field in nonevolutionary (i.e., standard psychological) analyses. *Historicity* refers to the EP assumption that natural selection shaped these modular cognitive mechanisms to produce adaptive behavior in the so-called EEA (“environment of evolutionary adaptedness”), meaning past environments of long duration and consistent selective pressures (Bowlby 1969; Symons 1987). *Adaptive specificity* holds that these modular products of our evolutionary history are designed to produce very specific adaptive outcomes: male preference for mates who are youthful, healthy, and beautiful, for example (Buss 1994). Finally, *environmental novelty* refers to the EP view that modern (post-Paleolithic) environments are characterized by an unprecedented degree of novelty, owing to extensive sociocultural change following the abandonment of a foraging way of life.

From these assumptions, evolutionary psychologists deduce the following consequences:

1. Valid adaptive (Darwinian) explanations of behavior must refer to genetically evolved psychological mechanisms linked to specific features of the EEA.
2. “Culture,” “learning,” “rational choice,” and “fitness maximizing” are insufficiently modular (without further specification) to be realistic cognitive or behavioral mechanisms.
3. Contemporary human behavior often involves responses to evolutionarily novel conditions using modular cognitive mechanisms adapted to the EEA, and hence some of these responses may be maladaptive.
4. Measuring fitness outcomes or correlates of contemporary behavioral patterns is irrelevant and misleading.

To date, the great bulk of research in EP has been focused on mating behavior, particularly mate preferences (reviewed in Buss 1994). Prominent work has also been done on violence, particularly in the contexts of male-male competition, male mate-guarding, and conflicts over parental investment in dependent young (e.g., Daly and Wilson 1988; Thornhill and Thornhill 1992). Surprisingly, very little EP research has actually focused on documenting the existence of modular cognitive mechanisms, though an exception is the work of Cosmides and Tooby on reasoning concerned with detecting cheaters in social exchange situations.

This topic of social exchange will serve here as a heuristic example of differing research strategies in the three approaches. The EP approach to social exchange has

of course focused on the notion that humans have a specialized cognitive mechanism for monitoring such exchange (Cosmides and Tooby 1989). The hypothesis is given an evolutionary basis by proposing that such exchanges were especially adaptive in the EEA—that is, among Pleistocene hunter-gatherers, who had both the ecological conditions favoring delayed reciprocity (particularly of hunted game) and the social and cognitive preadaptations needed to stabilize it against free riding (small groups, repeated opportunities for interaction, good memory and individual recognition) (Axelrod and Hamilton 1981; Trivers 1971).

Evidence adduced in favor of the hypothesis consists primarily of pencil-and-paper tests (based on the logic problem known as the Wason selection task) conducted among college students, although a sample of nonliterate Shiwiar Indian subjects in Amazonian Ecuador has also been tested (Tooby, personal communication).¹ The results indicate that narrative content involving social contracts and the possibility of cheating is a powerful predictor of success in these tests (Cosmides 1989; Cosmides and Tooby 1992; Gigerenzer and Hug 1992; but cf. Davies et al. 1995; Pollard 1990).

HUMAN BEHAVIORAL ECOLOGY

Behavioral ecology (BE) is the branch of evolutionary ecology concerned with tracing the link between ecological factors and adaptive behavior (Krebs and Davies 1997). This approach to the study of human populations began to appear about twenty years ago, and such studies have been reviewed several times (Borgerhoff Mulder 1991; Cronk 1991; Smith 1992; Smith and Winterhalder 1992; Winterhalder and Smith 2000).

The key assumptions of HBE (or BE in general) include its ecological selectionist logic, a “piecemeal” analytical approach, a reliance on modeling, a focus on “decision rules” or “conditional” strategies, and the so-called phenotypic gambit. *Ecological selectionism* consists of analyzing any behavioral phenomenon by asking “What are the ecological forces that select for behavior X?” The “ecological” part of this logic means that HBEs usually look to environmental features (e.g., resource density, competitor frequency) and examine the covariation in these features and the behavior of interest (e.g., territorial defense). The “selectionist” aspect means that predictions about this covariation are derived from expectations about what patterns we expect natural selection to favor. This of course sidesteps two complex issues (on which more below): Does natural selection act on this variation, and how? Do current selective forces correspond to the evolutionary past?

The *piecemeal approach* holds that complex socioecological phenomenon are fruitfully studied piece by piece—in a reductionist rather than holistic fashion. Thus, a complex problem such as explaining the marriage patterns in a population is broken down into a set of component decisions and constraints such as the

female preferences for mate characteristics, male preferences, the distribution of these characteristics in the population, the ecological and historical determinants of this distribution, and so on. This piecemeal analysis relies on a series of simple and general analytical *models* (e.g., the polygyny threshold model—Borgerhoff Mulder 1990; Orians 1969); the assumption is that such models are fruitful sources of testable hypotheses (e.g., the number of wives per male will be proportional to their wealth; a female will choose to marry the male who provides the greatest expected share of resources to her, hence equilibrating female fitness across polygynous and monogamous marriages).

HBE usually frames the study of adaptive design in terms of “decision rules” (Krebs 1978) or *conditional strategies*. These are abstract and somewhat metaphorical ways of conceiving the covariation of behavior and socioecological environment, having the general form “In context X, do α ; in context Y, switch to β .” Thus, HBEs tend to focus on explaining behavioral *variation* as adaptive responses to environmental variation; they assume that this adaptive variation (facultative behavior, phenotypic response) is governed by evolved mechanisms that instantiate the relevant conditional strategy or decision rule. This assumption, which takes a “black-box” approach to the actual mechanisms involved, is part of what Grafen (1984) terms the *phenotypic gambit*. This means taking a calculated risk to ignore the (generally unknown) details of inheritance (genetic or cultural), cognitive mechanisms, and phylogenetic history that may pertain to a given decision rule and behavioral domain in hopes that these don’t matter to the end result. Put another way, the phenotypic gambit posits that the genetic, phylogenetic, and cognitive constraints on phenotypic adaptation are minimal, and hence as a first approximation can be ignored in constructing models and generating or testing hypotheses.

Human behavioral ecologists draw several key conclusions from these assumptions, including:

1. Behavioral diversity is largely a result of diversity in the contemporary socioecological environment (rather than in contemporary variation in genes or cultural inheritance, or in past environments).
2. Adaptive relationships between behavior and environment may arise from many different mechanisms; hence HBE is generally agnostic about mechanisms (including the question of cognitive modularity).
3. Since humans are capable of rapid adaptive shifts in phenotype, they are likely to be well-adapted to most features of contemporary environments, and to exhibit relatively little adaptive lag.

These conclusions obviously conflict with some of those drawn by evolutionary psychology (EP) and dual inheritance theory (DIT), a point to which I will return.

Most HBE research has focused on subsistence and resource exchange (particularly in foraging societies), on parental investment (e.g., birth spacing, gender differences in parenting), and on reproductive strategies (e.g., polygyny vs. monogamy vs. polyandry) (reviews in Borgerhoff Mulder 1991; Cronk 1991; Smith and Winterhalder 1992; Winterhalder and Smith 2000).

As with EP, we can briefly examine the HBE analysis of social exchange as a heuristic example of this research strategy. Whereas EP has concerned itself with the cognitive mechanisms underlying social exchange, and tested for evidence of these in controlled experimental (but thus nonnaturalistic) circumstances, HBE research has focused on quantifying the behavioral occurrence, socioecological context, and fitness-correlated payoffs from food exchange in extant hunter-gatherer and horticultural populations (e.g., Berté 1988; Hames 1990, this volume; Kaplan and Hill 1985). Increasingly, this work is motivated by attempts to evaluate alternative models or hypotheses concerning the selective factors that may favor observed patterns of food transfer (Winterhalder 1996). The candidates include delayed reciprocity for risk reduction (Smith 1983, 1985, 1988; Smith and Boyd 1990; Winterhalder 1986, 1990), tolerated theft (Bliege Bird and Bird 1997; Blurton Jones 1984; Boone 1992; Hawkes 1992), trade of food for social benefits such as sexual access (Hawkes 1990, 1991, 1993; Kaplan et al. 1990), kin selection (Morgan 1979; Palmer 1991), and group selection (Wilson 1998). In light of this unresolved debate, it is interesting to note that EP analyses of social exchange assume that only the first of these mechanisms is at work and are not designed to test the competing assumptions just noted.

DUAL INHERITANCE THEORY

The dual inheritance (DIT) approach refers to studies that view culture and genes as providing separate (but linked) systems of inheritance, variation, and fitness effects—and hence of distinct but interacting evolutionary change. Reviews of this work can be found in Boyd and Richerson (1985), Durham (1990, 1991, 1992), Pulliam and Dunford (1980), and Richerson and Boyd (1992).

Key assumptions of DIT include cultural inheritance, multiple forces, population modeling, and codetermination. *Inheritance* refers to the idea that culture is information that is acquired socially—that it is a (nongenetic) system of inheritance. This is meant to contrast culture with information acquired through nonsocial learning, as well as genetically inherited information. Most DIT practitioners posit that the spread of cultural information or “memes” (Dawkins 1976) is affected by *multiple forces*: natural selection (differential fitness of culturally inherited variation), decision making (based on genetically or culturally evolved preferences and constraints, and subject to manipulation and coercion by others), and transmitter influence or prominence (since cultural “parents” need not be bio-

logical parents). These various forces or dynamics are analyzed via *modeling* that links individual characteristics (such as memes) with population-level processes (such as meme frequency), in a manner analogous to (and sometimes directly borrowed from) evolutionary population genetics. Finally, the *codetermination* assumption holds that human behavior is jointly shaped by genetic, cultural, and (nonsocial) environmental influences, thus advancing a form of explanatory pluralism notably lacking from the “purer” versions of EP and HBE.

Conclusions that DIT scholars deduce from these assumptions include the following:

1. Since culture exhibits the three characteristics required for evolution by natural selection (variation, heritability, fitness effects), cultural evolution can be analyzed using neo-Darwinian methods.
2. Since cultural inheritance differs from genetic inheritance in key ways (e.g., non-parental transmission, multiple transmission events over a lifetime), the evolutionary dynamics of culture will also differ in important but analytically understandable ways.
3. Genetically nonadaptive cultural evolution is possible, and it is more likely when the differences just referred to are most marked (e.g., modern bureaucratic societies and other hierarchical social/enculturation structures).

Thus, in contrast to classical forms of cultural evolutionism (e.g., White 1959; Sahllins and Service 1960) as well as what some term “evolutionary archaeology” (O’Brien 1996; cf. Boone and Smith 1998), DIT practitioners posit that cultural evolution is embedded in and constrained by genetically evolved psychological propensities. Indeed, one of the primary themes of DIT is the development of scenarios or models for the genetic evolution by natural selection of particular mechanisms of cultural transmission (see especially Boyd and Richerson 1985:98ff., 1995; Rogers 1988). But in contrast to classical sociobiology, or most varieties of EP and HBE, DIT holds that culture can sometimes evolve in directions quite different from what we would predict from genetic evolution alone, including genetically maladaptive directions. DIT is not, however, primarily a theory about how cultural evolution supersedes genetic evolution and takes humans down a maladaptive but independent pathway, as some of its critics as well as naive supporters too often claim. Indeed, the general thrust of both Durham’s (1991) version as well as recent work by Richerson and Boyd (1998, 1999) is that mechanisms of cultural evolution often find ways of *improving* on adaptive outcomes compared to what can be achieved by ordinary genetic evolution plus phenotypic adaptation.

To date, DIT has focused primarily on mathematical modeling of various possible patterns of cultural evolution or of gene-culture coevolution. Hence it is theoretically rich and sophisticated, but empirically impoverished; indeed, the most detailed empirical studies in the DIT literature seem to converge very closely to the HBE approach (Borgerhoff Mulder and Mitchell 1994).

In parallel with my discussions of EP and HBE, we can briefly consider DIT research on social exchange. Since collective action often involves systems of widespread and indirect reciprocity (e.g., serving as a soldier on behalf of one's society is reciprocated with various kinds of rewards to the soldier or his kin), it qualifies as a form of social exchange. Boyd and Richerson (1982, 1985, 1987) have constructed models of cultural group selection of such group-beneficial behaviors. These models show that cultural inheritance plus conformity transmission ("when in Rome, do as the Romans do") can in principle create and maintain significant between-group differences despite reasonable rates of migration between these groups, thus avoiding a major obstacle facing classical forms of genetic group selection.

The mechanism of group selection most commonly proposed in this regard is group dissolution due to warfare, with refugees from defeated groups being absorbed by allied groups; if culturally transmitted traits that favor socially altruistic traits (e.g., contributing to the collective good of military defense and offense) decrease the probability of group defeat and dissolution, then these could spread by cultural group selection (Peoples 1982). However, a recent examination of empirical evidence from highland New Guinea (Soltis et al. 1995), an area of chronic between-group hostilities, indicated that historical rates of group dissolution are probably too low to make this a plausible mechanism for the generation of a substantial amount of the variation in New Guinea in group-cooperative behavior. It remains a viable hypothesis to explain slower trends in cultural evolution (e.g., the rise of urban city-states), however (Richerson and Boyd 1999).

COMPETITION OR PLURALISM?

Given the distance between Darwin's general theory of evolutionary adaptation and the specifics of human behavior (as suggested in my epigraph from Washburn), the development of divergent styles in the evolutionary analysis of human behavior was perhaps inevitable. There are many plausible ways to go about filling the chasm between general theory and empirical data, and different "schools" have coalesced around those who pioneered various tracks through this terra incognita. In addition, this divergence reflects differing research traditions and academic disciplines—ethnography, cognitive psychology, evolutionary ecology, population genetics—that predate the emergence of modern evolutionary studies of human behavior. Indeed, it may be that the three-part division is found throughout the social and behavioral sciences: approaches that see behavior as a manifestation of underlying mental structures (e.g., psychoanalytic theory, structuralism, Chomskian linguistics), those that focus on determination by supra-individual structures (e.g., classical cultural determinism, classical sociology, Foucauldian theory), and those that model behavior in terms of costs and benefits (e.g., operant conditioning, rational choice theory, social exchange theory).²

Yet there is more to this divergence than simple cultural inertia or division of labor, for the differences between these three approaches reflect underlying fault lines concerning fundamental questions about the explanatory logic of Darwinism as applied to human behavior. As a result, the three approaches just surveyed have been portrayed by proponents of each as self-sufficient, and as alternatives to or competitors of the other approaches. But there are good reasons to see them as complementary as well (a point also made by Blurton Jones 1990 and Borgerhoff Mulder et al., 1997).

As summarized in Table 2.1, the three approaches differ in several ways. First, although all three ostensibly share the same goal of using Darwinian theory to analyze human behavior, in fact they identify different explananda (objects of explanation). EP's explanandum is the panhuman set of genetically evolved psychological predispositions that are believed to provide the "missing link" between evolution and behavior (Cosmides and Tooby 1987). These predispositions are presumed to take the form of cognitive algorithms or decision rules, in conformity with EP's parent discipline of cognitive psychology. The primary explanandum in HBE is observable patterns of behavior, with the goal of linking these patterns to environmental conditions (as eliciting factors) and to fitness-correlated payoffs (as reinforcing outcomes). For DIT, the explananda consist of culturally and genetically inherited information (memes and genes) that are shaped by evolutionary forces and that in turn shape cognitive algorithms and behavioral responses. Thus, DIT—following the tradition of its parent discipline of evolutionary genetics—focuses on the evolutionary equilibria and dynamics of heritable information, as well as the ways in which this information is transmitted.

Table 2.1. Summary comparison of the three styles of explanation.

	<i>Evolutionary Psychology</i>	<i>Behavioral Ecology</i>	<i>Dual Transmission Theory</i>
Explanandum:	Psychological mechanisms	Behavioral strategies	Cultural evolution
Key constraints:	Cognitive, genetic	Ecological, material	Structural, information
Temporal scale of adaptive change:	Long-term (genetic)	Short-term (phenotypic)	Medium-term (cultural)
Expected current adaptiveness:	Lowest	Highest	Intermediate
Hypothesis generation:	Informal inference	Optimality and ESS models	Population-level models
Hypothesis-testing methods:	Survey, lab experiment	Quantitative ethnographic observation	Mathematical modeling & simulation
Favored topics:	Mating, parenting, sex differences	Subsistence, reproductive strategies	Large-scale cooperation, maladaptation

Most evolutionary social scientists and biologists would agree that complete evolutionary explanations of behavior will include (i) heritable information that helps build (ii) psychological mechanisms, which in turn produce (iii) behavioral responses to (iv) environmental stimuli, resulting in (v) fitness effects that shape the evolutionary dynamics of (i) heritable information (see Figure 2.1). DIT focuses on culturally inherited components of (i) and its links to (ii) and (v); EP focuses on (ii) and its links to (iii) and especially (iv); and HBE focuses on (iii) with attention to (iv) and especially (v). While advocates of each approach may be all too human in claiming to have the best or only valid perspective on evolution and human behavior, a more dispassionate assessment might acknowledge that each approach contributes to understanding the entire set of relevant phenomena. Viewed in this light, a tentative case can be made for explanatory complementarity.

Second, the three approaches utilize different—but potentially complementary—methods of data collection and hypothesis testing. EP's hypothesized cognitive mechanisms are primarily inferred from questionnaires (surveys and paper-and-pencil psychological tests) and from lab experiments in which subjects interact with computer images, other subjects (or confederates), or in small groups. Again, all this conforms to the parent discipline of academic cognitive psychology. In contrast, HBE emphasizes ethnographic methods derived primarily from its parent discipline of anthropology (and secondarily from its other parent discipline of behavioral ecology).³ DIT's methods of data collection are underdeveloped, but hypothesis testing is likely to rely upon mathematical modeling (including simulations) as well as cross-cultural tests.

Each of these methods has strengths and weaknesses, and none of them seem tied in any deep way to the approaches with which they are primarily associated. Thus, questionnaires and experiments can generate large quantities of data and address domains in which observational data are difficult to collect (such as sexu-

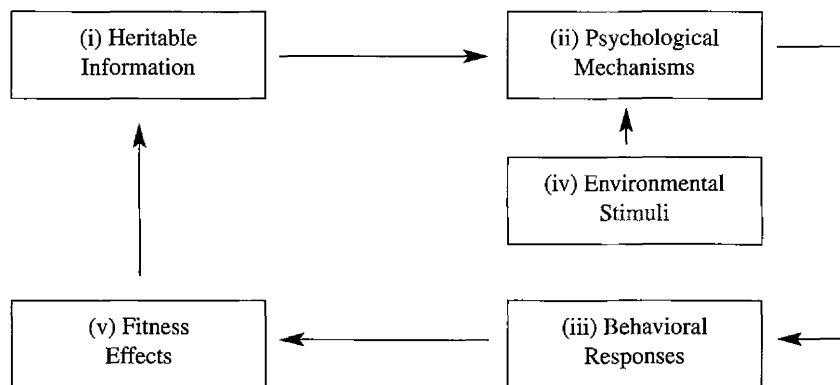


Figure 2.1. Causal foci and pathways in evolutionary analysis of behavior.

ality); on the other hand, these forms of data collection are subject to bias from deception and self-deception, and are sometimes of questionable relevance to “real-life” situations. Naturalistic observation uncovers context and provides concrete evidence of adaptive effects of phenotypic variants; yet it is vulnerable to the problems of sampling error and “phenotypic correlation” (i.e., confounding variables that mask the effects under investigation).⁴ Mathematical modeling and simulation can be powerful means of revealing nonintuitive outcomes from a set of assumptions, but they can be an ambiguous basis for hypothesis testing since they illuminate causality in simplified possible worlds rather than in complex real ones. Again, I see these points as supporting the argument for complementarity of the three approaches.

A third dimension in which the differences between our three approaches can be seen as complementary is the temporal scales over which they conceive of adaptive change. EP’s concern with psychological universals that evolved in past episodes of natural selection implies a longer time scale for adaptive change than that of the other two approaches. According to some of its proponents (e.g., Symons 1989; Tooby and Cosmides 1989, 1990), complex cognitive adaptations are likely to have taken shape in the Pleistocene or earlier, and to be maintained by phylogenetic inertia for millennia after the selective conditions that favored them have vanished. Although various critiques of this position have been published (e.g., Foley 1996; Irons 1990, 1998; Sherman and Reeve 1996; Turke 1990), it remains a plausible (if relatively untested) account of some patterns of human cognition and decision making.

Because HBE assumes that evolved mechanisms of phenotypic adaptation are quite flexible and broad—that we are adapted to a wide *range* of conditions rather than to a particular environmental state—its temporal scale for adaptive change is short-term, in behavioral rather than evolutionary time. Viewed this way, there should be as much complementarity as conflict between EP and HBE, despite the pronouncements of some: EP focuses on delineating adaptations that were genetically evolved in millennia past, while HBE focuses on how (at least some of) these adaptations may produce adaptive behavior in the present, responding to local and short-term environmental variation with matching phenotypic variation. The temporal scale of DIT is intermediate to these two extremes, given its focus on culturally heritable variation that is likely to evolve substantially faster than the complex cognitive mechanisms of EP but to adapt to changed conditions less quickly on average than the behavioral responses central to HBE.⁵

These complementarities between the three approaches are countered by some clear contradictions. One of these involves assumptions regarding key constraints on adaptation, while a second concerns the degree to which contemporary human behavior is predicted to be adaptive. Both of these flow quite logically from the differing explananda of the three approaches. Given EP’s focus on genetically evolved cognitive mechanisms, it is no surprise that the key constraints to achieving adaptive success are seen as cognitive and genetic. If human behavior is

guided by special-purpose cognitive algorithms that are genetically canalized and adapted to the EEA (see above), and if present social and natural environments are markedly different from this EEA, it follows that contemporary behavior may be frequently maladaptive. In the more extreme versions of this “adaptive lag” argument, humans in modern environments resemble computers trying to run new software on outdated operating systems. For example, men are viewed as following cognitive algorithms to pursue status and wealth which in the EEA translated into reproductive success, but now produce suboptimal fertility or sterile copulations because of contraception. (Indeed, there is some empirical support for such a view; see Kaplan et al. 1995 and Pérusse 1993.)

DIT’s concern with cultural transmission and the tradeoff between acquiring adaptive feedback via trial and error versus imitating the local practices (a simple form of cultural inheritance) lead it to view key adaptive constraints as informational (how hard is it to determine the states of the environment, and the local beliefs and practices?) and structural (who are the most likely sources of cultural information, and why?). Although some extreme views in the DIT literature suggest that memes are best viewed as “mind parasites” that replicate at the expense of their human hosts (e.g., Cullen 1995; Dawkins 1993; Lynch 1996), the dominant position has been that spread of maladaptive memes is a byproduct (though a regular and predictable one) of reliance on a system of cultural inheritance that on average enhances the fitness of those who possess it (Boyd and Richerson 1985, 1995; Durham 1976, 1991).

The HBE approach identifies the key constraints to adaptation as ecological and material: unpredictable variance in ecological conditions, limitations of social institutions or technology, and phenotypic (nonheritable) differences in power or circumstance. Cognitive and genetic, or structural and informational, constraints are rarely considered in this tradition, leading some critics to charge HBE with hyperadaptationism; whether this charge is justified or not, HBE clearly takes the most optimistic view of contemporary adaptiveness of human behavior. While committed to empirical tests that can in principle falsify any particular adaptationist hypothesis, HBE practitioners generally seem to expect that maladaptation will be the exception rather than the rule.

As I’ve already implied, many commentators have identified the key conflict between EP and HBE as revolving around the centrality of psychological mechanisms in evolutionary (adaptive) explanations. Since much ink has already been spilled on this topic, I will simply point out that HBE’s *agnosticism* regarding psychological mechanisms is not the same as a *denial* that they play a necessary role in any complete explanation of behavior. While some (e.g., Symons 1989) have seen this agnosticism as a misplaced fear of genetic reductionism, and others (e.g., Tooby and Cosmides 1992) as a variant of standard social science’s naive view of cognition, I think it is better seen as a venerable tradition in adaptationist studies, part of the “phenotypic gambit” noted earlier. That is, HBE focuses on “why” questions (Why did selection design this creature to respond to environmental

condition X with phenotypic adaptation a?) at the expense of considering “how” questions (What are the mechanisms that produce the phenotypic response?). If I’m correct, HBE should exhibit just as much agnosticism concerning physiological mechanisms as psychological ones—which I believe it does.⁶

The nub of the conflict between EP and DIT concerns the source of preferences and beliefs that inform adaptively significant decisions (Flinn 1997; Richerson and Boyd 1989; Rogers 1988). EP’s focus on genetically evolved panhuman cognitive algorithms tends to make its practitioners relatively hostile to the DIT view that humans acquire a substantial proportion of their beliefs and preferences through cultural inheritance, and that these beliefs and preferences can change through a process of cultural evolution. In contrast, HBE’s agnostic or ecumenical position regarding decision mechanisms creates less overt conflict with DIT, as does the fact that DIT practitioners are far more likely to have training and expertise in evolutionary ecology than in cognitive psychology.

But more detailed examination reveals that the HBE community is split on the issue of cultural evolution, with some granting it great importance while others express skepticism or even antipathy to the approach. Similarly, the EP community is far from monolithic in rejecting DIT. Indeed, common ground between the two approaches can be found in the fact that DIT is founded on the assumption that humans have genetically evolved psychological mechanisms to facilitate cultural adaptation, including such postulated algorithms as “conformity transmission” and “indirect bias” (Boyd and Richerson 1985). Thus, at least some DIT practitioners (Boyd and Richerson 1983, 1985; Pulliam and Dunford 1980) were doing EP before EP was cool—or had a name. Further complicating the matter is the importance that some EP practitioners ascribe to extensive cultural change (none dare call it evolution) since the time of the EEA, the source of EP skepticism concerning HBE attempts to portray post-Pleistocene behavioral innovations as adaptations. For if the divergence from the EEA is a product of cultural change, then culture is inescapably important in explaining contemporary human behavior.

In truth, the conflicts between the three approaches, so starkly drawn in some classical position papers (e.g., Durham 1979; Irons 1979; Symons 1989), are increasingly ambiguous and muted.⁷ I view this as one more piece of evidence that complementarity should replace conflict as the primary view (and mode) of their relations. Ultimately, these issues will have to be worked out via empirical research and theory development, rather than through the polemical pronouncements that have thus far dominated most attempts to confront them.

True complementarity will be at hand when researchers from the three traditions conduct their investigations at a variety of levels and using a variety of techniques—when cognitive algorithms are analyzed in naturalistic settings as well as with experiments or questionnaires, when phenotypic adaptation to socioecological variation is studied experimentally as well as ethnographically, and when models of cultural evolution are operationalized and tested against empirical data on a sustained basis. Evaluation of the relative efficacy of the three styles in explaining

human behavioral adaptation will be possible only when each of them has produced a substantial body of data on a single topic, so that we can compare (for example) the different predictions each generates concerning the adaptive significance of reduced family size under modernization (is it a maladaptive outcome of stone-age algorithms, a means of enhancing lineage fitness by preserving heritable wealth, or a product of cultural evolution when transmission of memes and genes is negatively correlated?).⁸

Even in areas where contradiction seems to trump complementarity, there may be considerable room for the latter. Thus, while it cannot be simultaneously true that a given instance or pattern of human behavior is a product of a genetically programmed cognitive algorithm that no longer produces adaptive results, a product of a culturally inherited meme that persists because it has high replication rate, and a product of phenotypic adaptation that is optimally geared to local environmental conditions, I see no reason to deny that each of these hypotheses could be true for *different* behavioral domains or instances.

In sum, it may turn out that each of our three approaches will have limited but significant success with different domains of human behavior. More optimistic, perhaps, is the hope that the not-too-distant future may see a synthesis of all three styles into a robust and pluralistic discipline focused on the evolutionary study of human behavior. A similar (if more elegantly phrased) prediction was in fact offered by Mel Konner (1982:xv) in *The Tangled Wing* some 15 years ago:

We prefer simple, clear explanations. This is understandable; we are busy with other things. We need theories that . . . transcend the complexities, paring away all that is irrelevant, leaving the elegant, decisive beauty of a Euclidean proof . . .

I offer no such theories. It is my belief that the failure of behavioral science up to the present day results, precisely, from the pursuit of them. Marxism, psychoanalysis, learning theory, structuralism, sociobiology—not a single one false in its essence, but each one false in its ambitions and in its condemnation of the others. A good textbook of human behavioral biology, which we will not have for another fifty years, will look not like Euclid's geometry—a magnificent edifice of proven propositions deriving from a set of simple assumptions—but more like a textbook of physiology or geology, each solution grounded in a separate body of facts and approached with a quiverful of different theories, with all the solutions connected in a great complex web.

SUMMARY

1. Three distinct approaches to evolutionary analysis of human behavior have developed in recent years: evolutionary psychology (EP), behavioral ecology (BE), and dual inheritance theory (DIT).

2. EP is based on the assumptions of modularity, historicity, adaptive specificity, and environmental specificity.

3. BE is based on ecological selectionism, piecemeal analysis, deductive modeling, conditional strategies (phenotypic adaptation), and the phenotypic gambit (ignoring the possible effects of inheritance, cognitive constraints, and phylogeny).

4. DIT assumes culture is a system of inheritance, that cultural change is affected by multiple forces (including genetically evolved psychological mechanisms), and that cultural evolution can be modeled mathematically.

5. Competition between the three approaches is fueled by differences in their assumptions, analytical methods, and alliances with other disciplines.

6. One key issue of contention is empirical: to what degree is contemporary human behavior adaptive, and what forces shape it to be adaptive or maladaptive?

7. Complementarity between the three styles may emerge from using complementary methods of investigation (e.g., observation vs. experiment), investigating different levels (e.g., psychological vs. behavioral), analyzing different constraints (cognitive, ecological, informational), examining adaptation on different time scales, or focusing on different behavioral domains.

ACKNOWLEDGMENTS

For helpful comments on drafts of this paper, I am grateful to Monique Borgerhoff Mulder, Rob Boyd, Nick Blurton Jones, Lee Cronk, Peter Richerson, Margo Wilson, Bruce Winterhalder, and a very gracious anonymous reviewer from the EP camp. Since I did not always follow the advice I was given, please do not hold any of the above responsible for what is wrong.

NOTES

1. The structure of the Wason test is as follows. There is a conditional statement of the form "If P, then Q." This statement is "conditional" in the sense that it is a claim that if condition P occurs, then result Q will occur. The statement may be true or false. The problem is to figure out if the evidence at hand supports the claim or not. The test usually involves a short narrative establishing the identity of P, Q, etc., followed by a presentation of four cards labeled with statements that signify "P," "Q," "not-P," and "not-Q" on their face, with the back of each card indicating whether the conditional rule ("If P, then Q; if not-P, then not-Q.") turned out to be true in the event or social interaction described in the narrative. The question before the subject is to decide the *minimum* set of cards that must be turned over in order to see if the rule has been violated; the solution is always to turn over *only* the cards marked "P" and "not-Q." Thus, the evidence Cosmides has assembled is that problems with a social contract narrative and rule ("If you take the benefit, then you pay the cost") are solved more readily (ca. 65–80% correct) than are problems associated with either a familiar (ca. 40%) or unfamiliar (ca. 20%) non-contract narrative.

2. I thank Lee Cronk (personal communication) for this suggestion.

3. Some HBE researchers more strongly influenced by nonhuman behavioral ecology are also motivated by a desire to make their methods and data conform to the standards set

by that field. On the other hand, the few extensions of HBE research into urban and industrialized settings (e.g., Betzig and Lombardo 1992; Kaplan et al. 1995; Pérusse 1993) have pragmatically adopted a questionnaire method of data collection reminiscent of sociological studies.

4. Phenotypic correlation occurs when a predicted effect of a determining variable on a phenotypic outcome is confounded by "uncontrolled" variables which also affect the same aspect of phenotype and are negatively correlated with the determining variable. For example, Lack's (1954) model of optimal clutch size has been used to generate the hypothesis that shorter interbirth intervals (IBI) put a strain on mother's ability to deliver food and care to her offspring, and hence increase the mortality risk for dependent children (Blurton Jones and Sibly 1978). The resultant prediction is that IBI length should be optimized to maximize the total number of surviving offspring, with most women exhibiting the optimal IBI. While data from the !Kung support this prediction (Blurton Jones 1986), data from the Ache do not (Hill and Hurtado 1996). As the latter note, the reason might well be due to phenotypic correlation: Ache mothers who for other reasons have relatively more resources at their disposal will have more resources per offspring and can thus "afford" a shorter IBI. The resultant phenotypic correlation means that short IBI can be positively (rather than negatively) correlated with offspring survival, even though Lack's tradeoff between more rapid reproduction and offspring survival applies. Indeed, Lack had to resort to some experimental manipulation of clutch size in order to counter such phenotypic correlation in his bird studies!

5. Those parts of DIT that deal with the genetic evolution of mechanisms of cultural transmission, or the coevolution of genetic and cultural variation, obviously assume a longer-term view of the evolutionary process.

6. This "physiological agnosticism" then indicates a gap to be filled, which of course has been done for a long time by biological anthropologists interested in human adaptability, including recent work in "reproductive ecology" (Ellison 1994; Wood 1994). However, in general this work does not ask questions about adaptive design informed by sociobiological theory à la Hamilton, Trivers, and Maynard Smith.

7. A parallel development is occurring in animal behavior studies; see, for example, the introductory chapter (among others) in the latest edition of Krebs and Davies (1997), or any issue of the journal *Behavioral Ecology*. However, not everyone is ready to bury the hatchet—*vide* Buss's recent (1995:9ff.) attack on Alexander, Betzig, Turke et al. under the heading "Why I am not a sociobiologist."

8. These three different predictions, generated by practitioners from each of the three schools, can be found in various sources, including Symons (1979), Rogers (1990), and Boyd and Richerson (1985).

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